

LENTIBULARIACEAE Richard

* Bladderwort Family

Garrett E. Crow

Herbs, annual or perennial, carnivorous. **Leaves** (or leaflike branches in *Utricularia*) basal and/or cauline, alternate, whorled, or in rosettes, simple or highly dissected (submersed aquatic *Utricularia* species); stipules absent; petiole present or absent; blade margins entire, or leaves highly dissected capillary segments (submersed aquatic *Utricularia* species).

Carnivorous traps: bladders or sticky glands. **Inflorescences** solitary flowers on scapes (*Pinguicula* and some *Utricularia*) or axillary or terminal, 1+-flowered racemes (most *Utricularia*).

Flowers weakly to strongly bilaterally symmetric; perianth and androecium hypogynous; sepals 2, [4], or 5, connate proximally, calyx 2-, [4-], or 5-lobed; petals 5, connate, corolla 2-lipped or appearing nearly regular and 5-lobed, lower lip spurred; stamens 2 and staminodes 0 or 2, antisepalous, distinct, adnate to corolla;; pistil 1, 2-carpellate, ovary superior, 1-locular, placentation free-central;; style 0 or 1; stigma 1, 2-lobed.

Fruits usually capsules, dehiscence usually circumscissile, by 2 or 4 valves, or 1 adaxial slit or pore [or irregular], rarely indehiscent. **Seeds** 1--many.

Genera 3, species ca. 334 (2 genera, 28 species in the flora): nearly worldwide.

Utricularia has about 228 species worldwide; *Pinguicula* has about 86 species; *Genlisea* Bentham & Hooker f. has about 30 species, 21 in Central and South America and the others in Africa (with 1 also in Madagascar). Tubers (in some species of Lentibulariaceae) are critical for surviving periods of desiccation. Many species are popular to grow as carnivorous novelties and have been the focal point of specialty plant societies worldwide. Some species are adapted to nutrient-poor acidic habitats, especially *Utricularia* and *Genlisea*; *Pinguicula* species are more frequently found in calcareous sites.

SELECTED REFERENCES Crow, G. E. and C. B. Hellquist. 1985. Aquatic vascular plants of New England: Part 8. Lentibulariaceae. New Hampshire Agric. Exp. Sta. Bull. 528: 1--19. Jobson, R. W. et al. 2003. Molecular phylogenetics of Lentibulariaceae inferred from plastid rps16 intron and trnL-F sequences: Implications for character evolution and biogeography. Syst. Bot. 28: 157--171.

1. Plants terrestrial; leaves in rosettes, simple, blade margins entire, involute, adaxial surfaces glandular-hairy; flowers solitary, bracts absent, calyx 5-lobed 1. *Pinguicula*, p. xxx

1. Plants aquatic or semi-terrestrial; leaves usually alternate or whorled, sometimes in rosettes, simple or highly dissected, margins entire or toothed, usually flat, adaxial surfaces glabrous; flowers usually in few+-flowered racemes (sometimes only 1 open at a time), sometimes solitary, subtended by a single bract, sometimes also a pair of bracteoles, calyx 2-lobed 2. *Utricularia*, p. xxx

1. PINGUICULA Linnaeus, Sp. Pl. 1: 17. 1753; Gen. Pl. ed. 5, 11. 1754 * Butterwort [Latin *pinguis*, fat, alluding to greasy feel due to secretions of glandular hairs on adaxial leaf surface]

Isoloba Rafinesque

Herbs, perennial [annual], terrestrial (leaves sometimes submersed). **Roots** present. **Stems** vertical. **Leaves** in rosettes, margins entire, strongly involute (often increasingly in-rolled toward apex, resulting in narrowly to broadly deltate outline), adaxial surface greasy, covered with sessile glandular hairs. **Inflorescences** solitary flowers on scapes; bracts and bracteoles absent. **Flowers**: calyx 5-lobed; corolla 2-lipped (northern taxa) or appearing nearly regular, with 5 spreading lobes at summit of corolla tube, lobes often incised or notched (southern taxa); palate absent (northern taxa) or

conspicuously formed at summit of tube, exerted beyond throat at base of lower lip, densely covered with clavate hairs (southern taxa); ovary glandular-pubescent. **Capsules** dehiscent by 2 or 4 valves. **Seeds** oblong to obpyramidal to cylindrical.

Species ca. 86 (9 in the flora): North America, Mexico, Central America, South America (to Tierra del Fuego), Europe, Asia.

Species of *Pinguicula* growing in cold climate regions produce buds (hibernacula) late in in the growing season; these buds produce new rosettes the following season, resulting in clusters of rosettes. Some species of *Pinguicula* utilize gemmipary, producing plantlets at leaf tips; plantlets are well rooted by the time parent leaf disintegrates. The "greasy" leaf surface results from a covering of subsessile glandular hairs (that capture insects) and obscure sessile glands (that secrete digestive enzymes).

SELECTED REFERENCES Casper, S. J. 1966. Monographie der Gattung *Pinguicula*. Biblioth. Bot. 127/128: 1--209. Cieslak, T. et al. 2005. Phylogenetic analysis of *Pinguicula* (Lentibulariaceae): Chloroplast DNA sequences and morphology support several geographically distinct radiations. Amer. J. Bot. 92: 1723--1736. Degtjareva, G. V. et al. 2004. Seed morphology in the genus *Pinguicula* (Lentibulariaceae) and its

relation to taxonomy and phylogeny. Bot. Jahrb. Syst. 125: 431-452. Degtjareva, G. V. et al. 2006. Morphology and nrITS phylogeny of the genus *Pinguicula* L. (Lentibulariaceae), with special attention to embryo evolution. Pl. Biol. (Stuttgart) 8: 778--790. Godfrey, R. K. and H. L. Stripling. 1961. A synopsis of *Pinguicula* (Lentibulariaceae) in the southeastern United States. Amer. Midl. Naturalist 66: 395--409. Kondo, K. and H. Shimai. 2006. Phylogenetic analysis of the northern *Pinguicula* (Lentibulariaceae) based on internal transcribed spacer (ITS) sequence. Acta Phytotax. Geobot. 57: 155--164. Wood, C. E. Jr. and R. K. Godfrey. 1957. *Pinguicula* (Lentibulariaceae) in the southeastern United States. Rhodora 59: 217--230.

1. Corollas 2-lipped, individual lobes not notched or incised; palate absent; Canada and northern United States.
 2. Rosettes 0.8--2(--3) cm across; corollas purple-veined from tube into spur, 6--10 mm (including spur), spur conic, (1.5--2.5--5(--6) mm; scapes usually white-villous proximally, densely glandular-pubescent distally 7. *Pinguicula villosa*
2. Rosettes 2.3--9 cm across; corollas not purple-veined (except within corolla tube on white blotch), (10--14--36 mm (including spur), spur slender to somewhat stout, (1--3--9(--11) mm; scapes

never villous, with short glandular hairs entire length or sparsely glandular above, glabrous below or sometimes glabrous throughout.

3. Corollas (10--14--22(--29) mm (including spur); spur (1--3--6(--7) mm; lobes of lower corolla lip oblong, not overlapping8. *Pinguicula vulgaris*
3. Corollas (14--17--36 mm (including spur); spur (4--5--9(-11) mm; lobes of lower corolla lip obovate-oblong, usually overlapping9. *Pinguicula macroceras*
1. Corollas appearing nearly regular and 5-lobed, individual lobes notched or incised 1+ more times (shallowly to deeply, sometimes giving appearance of several petals); palate present; southeastern United States.
 4. Corollas bright to pale yellow (with reddish to purplish veins in tube and spur), rarely white, lobes with 1(--3) notches3. *Pinguicula lutea*
 4. Corollas white to light blue, blue, light lavender, pink, or violet, sometimes yellow in throat or tube (veins prominent or not), lobes with 1 notch.
 5. Rosettes (0.8--1--3.5(--6) cm across; corollas (4--8--18(--22) mm diam., palate 1.5--2(--2.5) mm, included within corolla tube or barely exerted.....6. *Pinguicula pumila*

5. Rosettes mostly 4+ cm across; corollas mostly 18+ mm diam. (*P. ionantha* as small as 9 mm), palate (1.5--3--10 mm, conspicuously exerted from tube.

6. Corolla lobes about 2 times longer than wide, deeply notched or incised 1/3--1/2 length, spur (2--2.5--3(--4) mm; leaves reddish or reddish green (remaining green in shade but often suffused with red-purple especially along margins)

..... 4. *Pinguicula planifolia*

6. Corolla lobes to 1.2 times longer than wide to wider than long, shallowly to moderately notched to 1/4--1/3 (to 1/2 in *C. caerulea*) length, spur 2--7(--8) mm; leaves green.

[7. Shifted to left margin.—Ed.]

7. Scapes villous proximally for 1--4(--5) cm, sparsely to densely glandular-pubescent distally; corolla lobes strongly veined (veins blue), palate white to cream (to light greenish yellow); spur (4--5--7(--8) mm, violet to greenish yellow..... 1. *Pinguicula caerulea*

7. Scapes glabrous or sparsely glandular-pubescent, not villous, proximally, sparsely to more densely glandular-pubescent distally; corolla lobes not strongly veined; palate yellow, at least on upper portion, spur 2--5(--6) mm, yellow or yellowish green to tan-olive to yellow-olive to brown-olive to tannish brown.

8. Corollas without ring of white at base of lobes, tube lavender, with darker purple veins; hairs on inside lateral walls of corolla tube white; corolla lobes longer than broad.....2. *Pinguicula ionantha*
8. Corollas with ring of white at base of lobes, yellow within throat (best seen in fresh specimens), tube yellow, with brown or reddish brown veins; hairs on inside lateral walls of corolla tube yellow; corolla lobes nearly as broad as long or often broader5. *Pinguicula primuliflora*

1. *Pinguicula caerulea* Walter, Fl. Carol., 63. 1788 *

Blueflower butterwort **E**

Isoloba elatior (Michaux) Rafinesque; *Pinguicula elatior* Michaux

Plants: hibernacula not produced. **Rosettes** (2.5--4--9 cm

across. **Leaves** persisting year-round, yellowish green, ovate to obovate, longer leaves 1.2--3.4 cm (some with long non-glandular hairs along sunken midrib near base, crisscrossing midvein).

Scapes to 32 cm, densely villous (hairs multicellular)

proximally (to 1--4(--5) cm from base), sparsely to densely

glandular-pubescent distally. **Flowers:** calyx densely glandular,

lobes 4--5 mm; corolla usually blue to light blue or deep violet to pale violet, sometimes white, appearing nearly regular and 5-

lobed, 20--38 mm diam., lobes about as wide as long or often wider, with 1 notch 1/4--1/2 length, strongly veined, veins

blue; tube blue or violet to greenish yellow or white and

strongly veined, veins blue to violet; palate exserted, white to cream (to light greenish yellow), broad, blunt, (3--5--8 mm, densely covered with long whitish hairs; short-stalked clavate hairs absent along corolla ridge behind palate; eglandular hairs on lateral walls within tube white; spur violet to greenish yellow, usually thick, blunt at apex (sometimes slender, acute at apex), (4--5--7(--8) mm; filaments white, anthers pale yellow. **Capsules** globose, 4--5 mm (6--10 mm dehisced). **2n** = 32.

Flowering mid Jan--early Jun. Moist sandy soils, sandy peat, wet areas, flatwoods, pine savannas, adjacent ditches and roadsides; 0--200 m; Fla., Ga., N.C., S.C.

Pinguicula caerulea is found primarily on the Atlantic and Gulf coastal plains.

2. Pinguicula ionantha R. K. Godfrey, Amer. Midl. Naturalist 66: 405, fig. 6. 1961 * Violetflower butterwort **C E**

Plants terrestrial or leaves submersed; hibernacula not produced. **Rosettes** 6--15 cm across. Leaves persisting year-round, bright green, narrowly elliptic to lanceolate to oblanceolate to obovate, longer leaves 3--4.5(--6.5) cm. **Scapes** 9--19 cm, glabrous or sparsely glandular-pubescent proximally (not villous, eglandular hairs absent), more densely glandular

distally. **Flowers:** calyx glandular, lobes 4--5(--6) mm; corolla pale lavender to white with throat darker lavender within, without ring of white at base of lobes, appearing nearly regular and 5-lobed, 9--20(--23) mm diam., lobes usually longer than wide, length to 1.2 times width, with 1 shallow notch to 1/4(--1/3) length, not strongly veined; tube lavender to deep lavender, with darker purple veins, base of tube tapering abruptly to spur; palate strongly exserted, lower portion lavender or white, upper portion yellow, +/- cylindric, 3--4(--6) mm, lower portion glabrous, upper portion covered with yellow clavate hairs (tips reddening with age); darker golden short-stalked clavate hairs along inner corolla tube ridge behind palate; eglandular hairs on lateral walls within tube white; spur yellowish green to tan-olive to yellow-olive to brown-olive to tannish brown, linear-cylindric, 2.5--5(--6) mm; filaments pale violet to white, anthers pale yellow. **Capsules** globose, with depression, 4--5 mm (5--7.5 mm dehisced). **2n** = 22.

Flowering Feb--Apr. Boggy, mucky soils or wet sands, depressions in pine flatwoods, bogs, ditches, drainage canals; of conservation concern; 0--50 m; Fla.

Pinguicula ionantha is known only from the Florida panhandle, where it usually is found with *Pinguicula planifolia*.

3. Pinguicula lutea Walter, Fl. Carol., 63. 1788 *

Yellow butterwort **E**

Isoloba lutea (Walter) Rafinesque; *Pinguicula campanulata* Lamarck; *P. edentula* Hooker; *P. lutea* var. *edentula* (Hooker) A. de Candolle; *P. lutea* var. *minor* A. de Candolle

Plants: hibernacula not produced. **Rosettes** 4--9(--15) cm across. **Leaves** persisting year-round, yellowish green, broadly ovate to ovate to narrowly elliptic to lanceolate to somewhat deltoid, longer leaves 1.8--4 cm, margins ciliate at base. **Scapes** 15--25(--34) cm, densely glandular-pubescent (sometimes becoming less glandular proximally). **Flowers:** calyx densely glandular-pubescent, lobes 4--8 mm; corolla bright yellow to pale yellow, rarely white, appearing nearly regular and 5-lobed, (1--1.5--3(--4.5) mm diam.; lobes longer than wide, with 1(--3) notches to 1/3 length; tube yellow to yellowish green, with prominent reddish to purplish veins (especially prominent inside); palate strongly exserted, stout, blunt, 6--10 mm, densely covered with long yellow clavate hairs; yellow-orange short-stalked clavate hairs on corolla tube ridge behind palate; hairs on lateral walls within tube yellow; spur same color as tube, slender, tapering to acute apex, (3--4--8(--10) mm; filaments white, anthers pale yellow. **Capsules** globose, 4--6 mm (7--9 mm dehisced). **2n** = 32.

Flowering Feb--Apr. Wet to moist sandy, peaty, or mucky soils of bogs, depressions of pine flatwoods and pine savannas, adjacent ditches and roadsides; 0--200 m; Ala., Fla., Ga., La., Miss., N.C., S.C.

Pinguicula lutea is found primarily on the Atlantic and Gulf coastal plains. Plants with white corollas occur occasionally in the longleaf pine-saw palmetto flatwoods in the Apalachicola region of the Florida panhandle.

4. *Pinguicula planifolia* Chapman, Fl. South. U.S. ed. 3, 303. 1897 * Chapman's butterwort **E**

Plants terrestrial or leaves often submerged at flowering; hibernacula not produced, vegetative reproduction sometimes by gemmipary. **Rosettes** 5--18 cm across. **Leaves** persisting year-round, reddish or reddish green (remaining dull green in shade, often suffused with red-purple especially along margins), rather flat, elongate, oblong to narrowly elliptic to oblanceolate to narrowly lanceolate to ovate, longer leaves 3--10 cm, margins slightly inrolled except at apex. **Scapes** to 34 cm, weakly glandular-pubescent or glabrous on proximal 2/3, sparsely glandular-pubescent distally. **Flowers:** calyx sparsely glandular-pubescent or glabrous, lobes 3.2--5.4 mm; corolla lavender to violet to very pale lavender to nearly white,

somewhat darker lavender within throat, appearing nearly regular and 5-lobed, 15--36 mm diam., lobes about 2 times longer than wide, with 1 notch or incision 1/3--1/2 length; tube with reddish purple veins; palate exserted, oblong, 3--6 mm, covered with yellow clavate hairs (less densely than other southern species); darker golden short-stalked clavate hairs along inner corolla tube ridge behind palate; long eglandular hairs on lateral walls within tube white; spur olive-green to olive-lavender, sometimes yellowish green, short and thick, acute at apex, (2--2.5--3(--4)mm; filaments pale to deep violet, anthers yellow. **Capsules** globose 4--5 mm (5--7.7 mm dehisced). **2n** = 32.

Flowering Mar--Apr. Very wet sites, often marly substrates bogs, boggy flatwoods, seeps, margins of peaty ponds, ditches; 0--100 m; Ala., Fla., Miss.

Pinguicula planifolia, while often locally abundant, is geographically very restricted (Florida panhandle and the Gulf coastal plain of Alabama and Mississippi), and is vulnerable to habitat destruction; it needs conservation.

5. *Pinguicula primuliflora* C. E. Wood & R. K. Godfrey,
Rhodora 59: 219, figs. 1--7, 11--14, 30. 1957 * Southern
butterwort **E**

Plants: hibernacula not produced, vegetative reproduction frequently by gemmipary. **Rosettes** 4--12.5 cm across. **Leaves** persisting year-round, bright green, broadly lanceolate to ovate to narrowly elliptic to narrowly oblanceolate, longer leaves 2.3--7 cm. **Scapes** 8--17 cm, usually glabrous proximally (not villous, eglandular hairs absent), sparsely glandular-pubescent distally, more glandular at summit. **Flowers:** calyx glandular, lobes 2.5--4 mm; corolla white or light blue to light lavender with ring of white at base of corolla lobes just above yellow throat, appearing nearly regular and 5-lobed, (15--25--30 mm diam. (often not opening fully in morning), lobes about as wide as long or often wider, with 1 shallow notch to 1/4 length, not strongly veined; tube lemon yellow, with prominent reddish brown or brown veins (more prominent within, sometimes obscure externally), base abruptly truncated/auriculate at junction with spur (hidden by lower calyx lobes); palate exserted, yellow, cylindrical, (1.5--3--5 mm, covered with bright yellow hairs; darker golden short-stalked clavate hairs along inner corolla tube ridge behind palate; hairs on lateral walls within tube yellow (best seen in fresh specimens); spur yellow, usually thick and blunt at apex, sometimes slender, 2--5 mm; filaments white, anthers pale yellow. **Capsules** globose, with small depression, 4--6 mm. **2n** = 32.

Flowering late Feb--May. Shade, springy woods with *Sphagnum* or *Pallavicinia*, flowing water, peaty sands, peaty islands, tussocks in *Nyssa* swamps, bogs, depressions in pine flatwoods and savannas, springs along streams; 0--100 m; Ala., Fla., Ga., Miss.

Small specimens of *Pinguicula primuliflora* can be confused with larger plants of *P. pumila*; they can be recognized by scapes more glandular distally, and sparsely glandular to glabrous proximally, corollas with a ring of white at the base of the lobes (just above the corolla throat), and the bases of corolla tubes abruptly truncated at junction with the spur; scapes in *P. pumila* are strongly glandular to the base, corollas lack a white ring, and corolla tubes taper into the spur. The habitat is also unique for *P. primuliflora*, differing from all the other species of the Southeast in its affinity for sphagnum springs and streamlets in shady woods.

Pinguicula primuliflora is endemic to the southwestern corner of Georgia (possibly extirpated) and the Florida panhandle west along the Gulf Coastal Plain to Mississippi, in highly vulnerable habitat and is recognized throughout its greatly restricted range as needing conservation.

6. Pinguicula pumila Michaux, Fl. Bor.-Amer. 1: 11. 1803

* Small butterwort

Isoloba pumila (Michaux) Rafinesque; *Pinguicula australis*
Nuttall; *P. floridensis* Chapman; *P. pumila* var. *buswellii*
Moldenke

Plants: hibernacula not produced, vegetative reproduction
sometimes by gemmipary. **Rosettes** (0.8--1--3.5(--6) cm across.
Leaves persisting year-round, light green to dark green, ovate
to oblong, longer leaves (0.5--1--1.9 cm, long eglandular
ciliate hairs at base and along midvein. **Scapes** 3--10 cm,
glandular-pubescent to base. **Flowers:** calyx densely glandular,
lobes 2.5--3.5 mm; corolla dark blue to pale blue to lavender to
pink to white, without ring of white at base of lobes, yellow
within corolla throat, appearing nearly regular and 5-lobed, (4--
10--18(--22) mm diam., lobes about as wide as long, with 1
shallow to very shallow notch; tube pale yellow or violet
especially on upper portion, sometimes whitish on lower portion
(except darker-colored flowers), veins darker reddish brown or
purple and conspicuous into spur, base of tube tapering into
spur; palate included within tube or barely exserted, conic,
1.5--2(--2.5) mm, covered with short yellow clavate hairs;
darker golden short-stalked clavate hairs along inner corolla
tube ridge behind palate; eglandular hairs on lateral walls

within tube yellow; spur yellow, cylindric, thick, usually tapering abruptly to apex (occasionally slender, tapering to acute apex), 2--4(--5) mm, nearly as long as tube, curved or deflected away from scape; filaments white, anthers white to pale yellow. **Capsules** nearly globose, 2.5--4 mm. **2n** = 22.

Flowering Jan--Jun. Moist to wet calcareous sites, rocky or sandy soils, pond margins, edges of depressions of peaty pine savannas and flatwoods, margins of sandy, grassy hummocks, ditches and drainage canals; 0--150 m; Ala., Fla., Ga., La., Miss., N.C., Okla., S.C., Tex.; West Indies (Bahamas).

Pinguicula pumila is found on the Atlantic and Gulf coastal plains. Corolla color may vary widely within a single population; white-flowered plants occasionally are seen. More robust plants of *P. pumila* sometimes occur under favorable moisture conditions, and individuals with blue corolla lobes and yellow corolla tubes can be confused with 5. *P. primuliflora*; see the discussion under that species.

7. *Pinguicula villosa* Linnaeus, Sp. Pl. 1: 17. 1753 *

Hairy butterwort, grassette velue

Plants over-wintering by hibernacula. **Rosettes** 0.8--2(--3) cm across. **Leaves** not persistent, green, often suffused with red, especially abaxially, ciliate along petiole, ovate to obovate,

longer leaves 0.4--1 cm. **Scapes** 2.5--5.5 cm, usually white-villous on proximal 1/3--1/2, densely glandular-pubescent with shorter hairs distally, sometimes glabrescent in fruit.

Flowers: calyx glandular, lobes 1--1.5 mm; corolla light lavender to purple, lower lip often yellowish near base, conspicuous purple veins extending from corolla lips and tube into spur (remaining purple when flower color fades in drying), 2-lipped, 6--10 × 4--7 mm diam., lobes not notched or incised, those of lower lip oblong; palate absent; white to yellowish, multicellular hairs at base of lower lip and within throat; spur same color as tube, conic, blunt at tip, (1.5--2.5--5(--6) mm; filaments and anthers white. **Capsules** globose to pyriform, 2--4 mm. **2n** = 16.

Flowering Jun--Jul. Sphagnum bogs, muskegs, hummocks along streams and pools, arctic/timberline, turfy alpine tundra; 0--1400 m; Alta., B.C., Man., Nfld. and Labr. (Labr.), N.W.T., Nunavut, Ont., Que., Sask., Yukon; Alaska; Eurasia.

Pinguicula villosa populations with white corollas occasionally occur.

8. *Pinguicula vulgaris* Linnaeus, Sp. Pl. 1: 17. 1753 *
Common butterwort, bog-violet, grasette vulgaire **F**

Pinguicula acutifolia Michaux; *P. vulgaris* var. *pallida* Lange

Plants over-wintering by hibernacula. **Rosettes** 2.3--4.5(--6) cm across. **Leaves** not persistent, green to yellowish green, broadly lanceolate to oblanceolate,--longer leaves (1--1.5--3.5(--4) cm. **Scapes** 4--9 cm, usually glandular-pubescent throughout or weakly--glandular on distal 1/3--1/2, sometimes glabrous, glabrescent in fruit. **Flowers:** calyx--glandular to sparsely glandular-pubescent or glabrous, lobes (1--1.5--3 mm, lower pair connate 2/3 length; corolla violet to blue-violet to pale blue, not purple-veined except within tube on white blotch, 2-lipped, (10--14--22(--29) x 6--10(--15) mm diam., lobes not notched or incised, those of lower lip oblong, not overlapping; palate absent; long, white, multicellular hairs at base of lower lip and within throat on lateral and lower walls; spur same color as tube, slender, tapering to acute tip (occasionally short and stubby), (1--3--6(--7) mm; filaments and anthers white. **Capsules** globose to slightly pyriform, 4--5(--6) mm. **2n** = 64.

Flowering Jun--Jul. Wet rocks and rock ledges, gravelly shores, seeps, wet gravelly open sites, bogs, wet meadows, acidic or calcareous areas; 0--2300 m; Greenland; St. Pierre and Miquelon; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., Que., Sask., Yukon; Alaska, Maine, Mich., Minn., Mont., N.H., N.Y., Vt., Wis.; Europe; Asia.

Plants often form clusters by producing plantlets from short stolons arising from stems below the rosettes. In western North America, *P. vulgaris* tends to be distributed less commonly in coastal areas. Larger-flowered plants of *P. vulgaris* appearing more like *P. macroceras* occasionally occur in areas such as Greenland, Newfoundland and southern Labrador, along James Bay, the Northwest Territories, and Yukon. The two species appear to overlap in the Canadian Rockies and western Montana where *P. macroceras* tends to have lower corolla lobes that may be somewhat obovate but that often do not overlap. Some intermediate specimens occur in eastern Oregon and eastern Washington. Frequently specimens occur that are difficult to clearly place in one taxon or the other.

9. *Pinguicula macroceras* Link, Jahrb. Gewächsk. 1(3): 54.

1820 * Pacific Northwest butterwort **F**

Pinguicula macroceras subsp. *nortensis* J. Steiger & Rondeau; *P. microceras* Chamisso; *Pinguicula vulgaris* Linnaeus subsp. *macroceras* (Link) Calder & Roy L. Taylor

Plants over-wintering by hibernacula. **Rosettes** 3--9 cm across.

Leaves not persistent, reddish green with conspicuously darkened midvein (dried), broadly to narrowly lanceolate, oblanceolate or sometimes narrowly oblong, longer leaves 2--6 cm. **Scapes** 5.5--

10 cm, glabrous or sparsely glandular-pubescent, more glandular distally (junction with calyx). **Flowers:** calyx glandular-pubescent at base, lobes 2--3(--4.5) mm, lower pair usually connate 1/2 length; corolla violet to blue-violet to pale blue, not purple-veined except within tube on white blotch, 2-lipped, (14--17--36 x 12--20 mm diam.; lobes not notched or incised, those of lower lip obovate-oblong, usually overlapping; palate absent; long, white, multicellular hairs at base of lower lip and within throat on lateral and lower walls; spur same color as tube, somewhat stout, somewhat blunt at apex (sometimes slender and acute), (4--5--9(--11) mm; filaments and anthers white.

Capsules globose to slightly pyriform, 4--5 mm. **2n** = 64.

Flowering Apr--Aug. Wet rocks and cliffs, seeps, boggy sites, with sphagnum moss; 0--2500 m; Alta., B.C., Yukon; Alaska, Calif., Mont., Oreg., Wash.; e Asia (Japan, Russian Far East).

Morphological distinction of the large-flowered plants of *P. macroceras* from *P. vulgaris* is not consistent, and has led some botanists to treat *P. macroceras* as a subsp. of *P. vulgaris*. Based on molecular studies within *Pinguicula* (T. Cieslak et al. 2005; K. Kondo and H. Shimai 2006), *P. macroceras* is recognized as a distinct species. *Pinguicula macroceras* tends to occur at mid elevations in the mountains and along

coasts, ranging from northern California to the Aleutian Islands, and extending to the Russian Far East and northern Japan. Populations from the Canadian Rockies (Banff/Jasper), Montana and eastern Oregon/Washington, often treated as *P. vulgaris* but having the larger flowers of *P. macroceras*, were treated by S. J. Casper (1962) as inland populations of *P. macroceras*. In general, these plants with larger flowers have a central corolla lobe that does not overlap the two lateral lobes (as is more typical for this taxon), the spurs are sometimes shorter than typical, and the leaves tend to be greenish (rather than reddish).

Some populations, primarily from the Aleutian Islands, Alaska, having large flowers but short stubby spurs (3--4 mm), have been called *Pinguicula microceras* Chamisso. Within the same populations both long-spurred and short-spurred plants occur. Furthermore, some individual specimens exhibit flowers with both short and longer spurs on the same plant, thus no infraspecific taxon is herein recognized. S. J. Casper (1962) showed that these plants fall within the range of variability of *P. macroceras*, and although he used the name *P. macroceras* var. *microceras* in that paper, the nomenclatural transfer was never formally made, nor was it taxonomically recognized in his later monograph (Casper 1966).

Populations restricted to rocky serpentine seeps and stream drainages in northern California and southwestern Oregon have been described as subsp. *nortensis*, distinguished by calyx lobes blunt-tipped, the central lobe of the lower corolla lip oblong, with lateral lobes obovate and not overlapping, and the spur 6--11 mm. It is recognized that plants of various species growing on serpentine may exhibit some morphological variation differing from other populations; however, this appears to be within the overall range of variability *P. macroceras* across its geographic distribution, and thus is not recognized taxonomically here.

White-flowered plants from Attu Island, in the Aleutians, have been described as *Pinguicula macroceras* forma *alba* Casper.

2. UTRICULARIA Linnaeus, Sp. Pl. 1: 18. 1753; Gen. Pl. ed. 5, 11. 1754 * Bladderwort [Latin *utriculus*, little sac, bag, or bladder, alluding to carnivorous traps]

Herbs, annual or perennial, submersed aquatic, semi-aquatic and amphibious [or epiphytic]. **Roots** absent (plants often anchored by rhizoids or stolons). **Stems** stolons, most giving rise to leaves (or leaflike branches); in some species, specialized stolons bearing bladders, suspended in water or anchored in substrate. **Leaves** (or modified leaflike branches) alternate or

whorled, sometimes in rosettes, usually dissected and bearing bladders, or sometimes simple and bladders borne separately from leaves, margins entire or toothed, flat; bladders ovoid to globose. **Inflorescences** usually racemes, sometimes solitary flowers; bract 1 (2 in *U. resupinata*) per flower; bracteoles 0 or 2. **Flowers:** calyx 2-lobed; corolla 2-lipped, lower lip entire to lobed, usually with conspicuous, raised, swollen palate (umbo) at base; ovary glabrous. **Capsules** dehiscent by 2 valves, 1 adaxial slit or pore, or circumscissile, rarely indehiscent. **Seeds** subglobose to cylindrical (sometimes angular).
x = 7, 9, 10, 11.

Species ca. 228 (19 in the flora): nearly worldwide; tropical to cold temperate.

Aquatic species of *Utricularia* in cold temperate regions perennate by turions (winter buds, hibernacula); these are usually distinctive by species. Semi-terrestrial and tropical epiphytic species usually develop tubers by which they survive dry conditions. Plants in this genus lack roots; the aquatic species are often free-floating or anchor by rhizoids or stolons. Bladders, which are carnivorous suction-traps, bear external "trigger" appendages associated with trap mouths and internal trap glands, comprised of 2-fid trichomes (few, adjacent to trap opening) and 4-fid trichomes (abundant,

associated with setting trap, secreting enzymes and absorbing nutrients). In aquatic species, flower scapes are thickened at water surface by development of aerenchyma.

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1. Plants semi-aquatic, in wetlands or anchored on wet shores (appearing semiterrestrial), typically only flowers and scapes visible (leaves, when present, very slender, terete, linear to thin, obovate to oblanceolate).
2. Corollas (except sometimes lower lip or palate) purple, violet, lavender, or mauve to pink or nearly white (sometimes white or yellow).
3. Inflorescences usually (2--)6--10-flowered racemes, flowers rarely solitary; each flower subtended by 1 bract and 2 bracteoles; scape scales present; corollas violet or mauve to pink to nearly white (sometimes white or yellow), often with white-bordered yellow spot at base of lower lip (on palate); lower lip distinctly 3-lobed; spur (1.5--)2--3 times longer than lower lip; leaf blades narrowly to broadly obovate or nearly orbiculate, not septate 1. *Utricularia amethystina*

3. Inflorescences 1-flowered; each flower subtended by 2
opposite, basally connate bracts; scape scales absent;
corollas light purple to rose-pink (rarely completely white),
usually with cream spot at base of lower lip (on palate);
lower lip obscurely 3-lobed; spur 1/2 as long as lower lip;
leaf blades linear-subulate to filiform, distinctly septate
(sometimes septa only 1--2, toward apex)
..... 15. *Utricularia resupinata*
2. Corollas yellow to greenish yellow, lower lip or palate sometimes
red-streaked.
4. Bracts and calyx lobes red, margins fimbriate..... 16. *Utricularia simulans*
4. Bracts and calyx lobes usually green (yellow in *U. cornuta*,
bracts purple in *U. juncea*), margins entire.
5. Corollas pale yellow to greenish yellow, with
conspicuous veins, lower lip with red streaks at base,
continuing into spur, palate usually red-streaked;
spur usually with shallow notch at apex, sometimes
obscurely 3-fid; stolons radiating from base of
inflorescence, whitish, bearing rhizoids
..... 17. *Utricularia striata* (in part)
5. Corollas yellow, without conspicuous veins (palate
red-streaked in *U. gibba*); spur not notched at apex

(sometimes slightly denticulate in *U. subulata*); base of inflorescence not bearing radiating stolons.

6. Upper corolla lip 3-lobed, slightly larger than lower lip 6. *Utricularia gibba* (in part)

6. Upper corolla lip unlobed, smaller than lower lip (longer in *U. amethystina*).

[7. Shifted to left margin.—Ed.]

7. Bracts and scape scales peltate; flowers subtended by a bract, bracteoles absent; spur inconspicuous, about as long as, and appressed to, lower corolla lip, often reddish; palate 2-lobed18. *Utricularia subulata*

7. Bracts and scape scales basifixed; flowers subtended by a bract and 2 bracteoles; spur conspicuous, longer than lower lip and strongly divergent from lip, never reddish; palate a broadly humped or hood-shaped.

8. Inflorescences congested, (1--3--5(--9))-flowered, usually clustered distally; corollas 15--25(--30) mm, spur 7--12(--14) mm; scapes green to yellowish green, stout, 0.5--1.5 mm diam. near base.....2. *Utricularia cornuta*

8. Inflorescences elongate, several--many-flowered, usually widely spaced along scape; corollas 9--15 mm, spur 4--6(--7) mm; scapes greenish purple to purple, slender, wiry, 0.4--1 mm diam. near base9. *Utricularia juncea*

1. Plants aquatic, submersed, unattached (rootless) or creeping over substrate (sometimes stranded on mud, appearing anchored); leaves divided into filiform to capillary segments (absent in *U. olivacea*).
9. Leaves whorled; bladders borne only at tips of leaf segments; corollas usually purple or pink, rarely white (lower lip with yellow blotch at base), lateral lobes of lower lip saccate
..... 13. *Utricularia purpurea*
9. Leaves alternate (absent in *U. olivacea*); bladders scattered on leaves and/or on stolons; corollas yellow or white (lips or palate sometimes with red or purple veins, streaks, or dots), lateral lobes of lower lip, if present, not saccate.
10. Scapes subtended by inflated, floating branches.
 11. Racemes (3--9--14(--18))-flowered; pedicels 10--35 mm, strongly recurved in fruit; corollas bright yellow, spur distinctly notched at apex; inflated branches 3--8 cm; individual float branches: margins tapering to scape; main stem 2--3 mm diam. (at 5 cm proximal to floats); leaves on submersed stolons divided into unequal primary segments, much-branched, bushy; bladders of 2 sizes, 1.5--2(--3) mm and 0.7--1 mm
..... 7. *Utricularia inflata*

11. Racemes (1--3 or 4(or 5)-flowered; pedicels 2--18 mm, ascending in fruit (rarely recurved); corollas dull yellow, spur rounded at apex, rarely with slight notch; inflated branches 1--4 cm; individual float branches: margins parallel most of length; main stem to 0.3--0.7(--1) mm diam. (at 5 cm proximal to floats); leaves on submersed stolons divided into 2 equal primary segments, less densely branched, not bushy; bladders of one size, 1.5--2 mm

.....14. *Utricularia radiata*

10. Scapes not subtended by inflated, floating branches.

[12. Shifted to left margin.—Ed.]

12. Stolons dimorphic, some whitish, bearing bladders (often buried in substrate), others green, bearing dissected leaves with no or 1--few bladders (fewer bladders than on non-green stolons).
13. Green leafy branches cylindric in outline (foxtail-like); leaf segments fine, terete, narrower beyond each dichotomy, ultimate divisions filiform, midveins not visible; bracts and scape scales not auriculate at base; corolla lips nearly equal length or upper slightly longer than lower.
14. Plants in deep water; green leafy branches to 40 cm long, 2--5 cm diam.; scapes flexuous, sometimes flattened, 2--3 mm diam.; corollas bright yellow, with red streaks on

palate but not on lower lip; spur (4--)4.5--6 mm, slightly

shorter to slightly longer than lower lip, apex blunt....3. *Utricularia floridana*

14. Plants in shallow water (some appearing terrestrial when stranded if water recedes); green leafy branches to 10 cm long, 1--1.5(--2) cm diam.; scapes erect, slender-wiry, 1 mm diam.; corollas pale to greenish yellow, with red streaks on lower lip and usually on palate; spur (5--)6--9 mm, 3/4 as long as to slightly longer than lower lip, apex usually notched, sometimes obscurely 3-fid..17. *Utricularia striata* (in part)

13. Green leafy branches flat, leaf segments flat, +/- same width throughout, ultimate divisions flat, midveins visible; bracts and scape scales conspicuously auriculate at base; corolla lower lip length 2+ times upper lip.

15. Corollas bright yellow, spur slightly shorter than lower lip, slender-cylindric, narrowed, constricted at base, +/- appressed to lower lip; bladders (1.5--)2.5--5.5 mm; leaf ultimate segments toothed, teeth (5--)9--12(--20), apex +/- obtuse; turions oblong, 7--11(--15) mm, setulose with white bristles on margins of scalelike leaves, appearing whitish on herbarium specimens

.....8. *Utricularia intermedia*

15. Corollas light or pale yellow, spur 1/5--1/2 as long as lower lip, saccate, broadly conic, or short-conic to pyramidal,

broad at base, not well defined (*U. minor*) or oriented at 45°--90° angle to lower lip (*U. ochroleuca*); bladders 0.3--2.2(--3.8) mm; leaf ultimate segments entire or sparsely toothed with (1--)3--6(--9) setulose teeth, apex acute; winter buds (turions), when present, globose-ovoid, (1.5--)2--4 mm, not or only weakly setulose (appearing naked, green).

16. Bracts and scape scales purplish; corollas: lateral margins of lower lip strongly curved downward; palate obscure, elongate, with slightly raised lateral margins; ultimate leaf segments entire or, if sparsely denticulate, then only microscopically setulose

.....10. *Utricularia minor* (in part)

16. Bracts and scape scales green; corollas: lateral margins of lower lip nearly flat to slightly curved upward or slightly deflexed; palate prominent, rounded; ultimate leaf segments usually sparsely toothed, weakly setulose, rarely entire..... 11. *Utricularia ochroleuca*

12. Stolons monomorphic, green, leaves bearing bladders.

17. Corollas creamy-white-translucent, (1--)2--2.3(--3.5) mm; leaves absent (vegetative portion minute, delicate, green stolons coiled at

tips, plants often entangled with other submersed vegetation)

.....12. *Utricularia olivacea*

17. Corollas yellow, 3.5--20 mm; leaves present.

18. Corollas pale yellow, lower lip purplish tinged or striped near base; lower corolla lip lateral margins strongly recurved; spur nearly lacking, 1.5--3.2 mm, saccate or broadly conic; bracts auriculate, purplish 10. *Utricularia minor* (in part)

18. Corollas yellow, often with red or reddish brown veins or streaks on upper lip or palate; lower corolla lip lateral margins spreading; spur 2--9 mm, broadly to narrowly conic to cylindrical; bracts not auriculate (sometimes auriculate in *U. vulgaris*), green.

19. Stolons flat, 1--4 mm wide, branching into usually dimorphic or trimorphic branch systems; leaf ultimate segments capillary (readily collapsing when withdrawn from water); spur apex notched; capsules indehiscent 4. *Utricularia foliosa*

19. Stolons terete, 0.5--1.5 mm diam., +/- monomorphic; leaf ultimate segments filiform (but not capillary); spur apex not notched; capsules dehiscent.

20. Stolons mostly less than 30 cm (to 30 cm in *U. gibba*); leaves divided 1--4(--8) times; racemes (1 or)2 or 3(--6)-flowered; upper corolla lip 3-

lobed, larger than lower lip; plants usually entangled among floating vegetation, or submersed, creeping over substrate (or, if stranded, then with flowers exposed above surface and vegetative portion usually buried in wet mud/sand)..... 6. *Utricularia gibba* (in part)

20. Stolons mostly 30--100+ cm; leaves divided 6+ times; racemes 2--15-flowered; upper corolla lip unlobed or slightly notched, smaller than lower lip; plants submersed and free-floating, usually not tangled among other vegetation.

21. Racemes 2--5(--8)-flowered; corollas not red-streaked or -veined, lower lip distinctly 3-lobed; apetalous cleistogamous flowers 1 or 2, 1.5--2.5 mm diam., at base of scape (sometimes only cleistogamous flowers present); leafy branches 1-3.5 cm diam.; leaf ultimate segments: margins entire or sparsely and inconspicuously setulose 5. *Utricularia geminiscapa*

21. Racemes (3--6--15-flowered; corolla
with palate red- or reddish brown-
veined, lower lip unlobed; cleistogamous
flowers absent; leafy branches 3--12 cm
diam.; leaf ultimate segments: margins
conspicuously setulose (with or without
teeth) 19. *Utricularia vulgaris*

1. *Utricularia amethystina* Salzmänn ex A. St.-Hilaire &
Girard, Compt. Rend. Hebd. Séances Acad. Sci. 7: 870. 1838 (as
amethystina) * Florida purple bladderwort

Calpidisca amethystina (Salzmänn ex A. St.-Hilaire & Girard)
Barnhart; *C. modesta* (A. de Candolle) Barnhart; *C. standleyae*
Barnhart; *Utricularia modesta* A. de Candolle

Plants annual or perennial, semiterrestrial. **Stolons** few,
branched, filiform, to several cm, 0.2 mm diam. **Leaves** in basal
rosettes; petiole to 2.5 cm; blade narrowly to broadly obovate
or nearly orbiculate, 2.5--6 mm wide, not septate, membranous,
with numerous anastomosing veins. **Bladders** on stolons, usually
buried within substrate, 1--1.2 mm. **Scapes** 1.5--9 cm; scales
present, basifixed, 1 mm; bracts basifixed, ovate or ovate-
deltate, 1 mm; bracteoles 2, adnate to bract 1/2 length or more,
bract appearing 3-fid. **Inflorescences** racemes, (1 or) 2--6(--

10)-flowered. **Pedicels** ascending, usually 5--15 mm. **Flowers:** calyx 1.5--3 mm; corolla violet, lavender, or mauve to pink or nearly white (sometimes white or yellow), often with white-bordered yellow spot at base of lower lip (on palate); 1.5--3.2--20 x 3--10 mm (very variable in size); lower lip distinctly 3-lobed; upper lip deflected, oblong to oblong-elliptic, unlobed (or occasionally shallowly notched), shorter than lower lip, apex rounded; palate prominent, 2-lobed, papillate (sometimes with stipitate glands); spur same color as rest of corolla, narrowly cylindrical, slender, (1.5--2--3 times as long as lower lip, apex tapering to acute. **Capsules** globose, 1.5--2.5 mm, wall thick, hard, dehiscence bivalvate.

Flowering Jan. Wet pine flatwoods; 0--20 m; Fla.; Mexico; Central America; South America.

P. Taylor (1989) noted that *Utricularia amethystina* is a difficult and incredibly polymorphic species. The North American specimens, originally described as *Calpidisca standleyae* Barnhart, are documented from only Collier and Lee counties and are extremely small for the species. This widespread neotropical species has not been seen in Florida since it was collected in 1946, and has likely become extirpated.

2. Utricularia cornuta Michaux, Fl. Bor.-Amer. 1: 12. 1803

* Horned bladderwort, utriculaire cornue

Stomoisia cornuta (Michaux) Rafinesque

Plants perennial, semiaquatic/semiterrestrial. **Stolons**

numerous, not radiating from inflorescence base, developing a delicate branch system within substrate, filiform, to several cm, ca. 0.2 mm diam. **Leaves** arising singly (often not seen), narrowly linear, terete, gradually tapering to a long point when submerged, when stranded becoming more straplike, flattened toward tip, or often withering away. **Bladders** on stolons, rhizoids, and leaves within substrate, 0.3--0.8 mm. **Scapes** green to yellowish green, stout, 12--38 cm, 0.5--1.5 mm diam. near base; scales present, basifixed, 1.2--2.5 mm; bracts basifixed, yellowish, broadly ovate, 1.6--2.8 mm, margins entire, apex acute; bracteoles 2, linear, 1.9--3 mm, slightly longer than the bracts. **Inflorescences** racemes, appearing spicate, (1--)3--5(--9)-flowered, congested, flowers usually clustered distally. **Pedicels** erect, 1--2 mm (flowers subsessile, pedicels shorter than or equal to bracts and bracteoles). **Flowers:** calyx yellow, 3--5(--7) mm, margins entire; corolla yellow, without conspicuous veins, 15--25(--30) x (4--)9--12(--17) mm; lower lip unlobed, lateral margins strongly deflexed; upper lip with sides curved backward, obovate

to broadly oblong from a narrow base, unlobed, smaller than lower lip, apex rounded or shallowly notched; palate comprising most of lower lip, broadly humped or hood-shaped, pubescence of short papillae; spur same color as rest of corolla, strongly divergent from lower lip, not clearly distinct from tube, conic, very slender, conspicuously curved, 7--12(--14) mm, longer than lower lip, apex long-tapering to acute. **Capsules** ovoid-pyriform, 3.5--4.5 mm, wall thick, hard, dehiscence by 1 longitudinal adaxial slit. **2n** = 18.

Flowering Apr--Aug, Nov. Shallow water, bogs, sandy-peaty margins of ponds, wet pine savannas, flatwoods, cypress pond borders, sandy alluvium, peaty ditches; 0--400 m; St. Pierre and Miquelon; Alta., Man., N.B., Nfld. and Labr., N.S., Ont., P.E.I., Que., Sask.; Ala., Ark., Conn., Del., Fla., Ga., Ill., Ind., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., N.H., N.J., N.Y., N.C., Ohio, Pa., R.I., S.C., Tenn., Tex., Vt., Va., W.Va., Wis.; West Indies (Bahamas, Cuba).

3. Utricularia floridana Nash, Bull. Torrey Bot. Club 23:

105. 1896 * Florida yellow bladderwort **E**

Plants perennial, aquatic, in deep water, anchored in loose, silty substrate. **Stolons** dimorphic: some whitish, slender. subterranean branches within silty substrate or submersed and

suspended branches, others green, leafy, cylindric branches (foxtail-like), to 40 cm, 2--6 cm diam., slender, terete.

Leaves alternate, dimorphic, subterranean leaves achlorophyllous, divided into filiform segments with apical setae, to 20 mm, photosynthetic leaves highly divided, to 30 mm, segments fine, terete, narrower beyond each dichotomy, ultimate segments filiform, midvein not visible. **Bladders** primarily on whitish, subterranean stolons, none (or very few) on green stolons, 1--2(--3) mm. **Scapes** not subtended by inflated, floating branches, flexuous, sometimes flattened, long (often emergent from as deep as 1 m), 2--3 mm diam.; scales present or absent, basifixed, similar to or smaller than bracts, base not auriculate; bracts basifixed, (1.5--2--3) mm, base not auriculate, apex truncate and denticulate (often 3-denticulate) or broadly tapering to a tooth; bracteoles 0. Inflorescences racemes, 5--20-flowered. **Pedicels** ascending, spreading, or slightly curved (not distinctly recurved), 7--20 mm. **Flowers:** calyx ovate, 2.5--4 mm, corolla bright yellow with red-streaks on palate but not on lower lip, 8--20 x 9--15 mm; lower lip shallowly 3-lobed, lateral lobes not saccate; upper lip nearly round, shallowly 3-lobed, slightly longer than lower lip, apex rounded; palate conspicuously swollen, 2-lobed-wrinkled, densely pubescent; spur yellow, +/- appressed to lower lip, narrowly

cylindric, somewhat S-shaped, with slight constriction at bend, tip deflected, (4--4.5--6 mm, slightly shorter to slightly longer than lower lip, apex blunt. **Capsules** globose, 4.5--8 mm, wall thick, fleshy, dehiscence bivalvate.

Flowering Mar--Oct. Submersed in quiet waters of lakes and ponds to 1 m deep (especially karst-formed, with little other vegetation); 0--100 m; Ala., Fla., Ga., S.C.

Utricularia floridana is found on the Atlantic and Gulf coastal plains.

4. Utricularia foliosa Linnaeus, Sp. Pl. 1: 18. 1753 *

Leafy bladderwort

Utricularia mixta Barnhart; *U. oligosperma* A. St.-Hilaire

Plants perennial, aquatic. **Stolons** (principal) green, branching into usually dimorphic or trimorphic branch systems of varying lengths (some bearing numerous bladders and others bearing few or none), elongate, flat, to several 100 cm, 1--4 mm diam.

Leaves alternate, primary rachis 20--30(--45) cm, secondary divisions numerous, ultimate segments exceedingly delicate, fine, capillary, readily collapsing when withdrawn from water, very mucilaginous. **Bladders** on leaves, scattered, 0.7--2 mm.

Scapes not subtended by inflated, floating branches, 7--45 cm; scales present, basifixed, 3--3.5 mm; bracts basifixed, green,

clasping pedicel, broadly ovate, 1.8--4 mm, base not auriculate, apex rounded to slightly acute; bracteoles 0. **Inflorescences** racemes, (3--7--15(--20))-flowered, congested, flowers +/- clustered distally. **Pedicels** spreading to ascending at anthesis, elongating and recurved in fruit, 7--21 mm. **Flowers:** calyx 3--6 mm; corolla yellow, often with red veins on inner surface of upper lip and red-streaks on palate, 8--16 × 10--20 mm; lower lip broadly 2-lobed or slightly 3-lobed, lateral lobes not saccate, lateral margins broadly spreading; upper lip orbiculate or nearly transversely elliptic, unlobed, smaller than lower lip, apex rounded; palate swollen, sparsely papillate; spur yellow, narrowly conic, straight, 4--7 mm, sometimes much shorter than or equal to lower lip, apex notched. **Capsules** globose, (4.5--5--8(--10) mm, walls thick, fleshy, indehiscent. **2n** = 42.

Flowering Jan--Dec. Ponds, pools, swamps, marshes, canals, drainage ditches; Fla., Ga., La., Miss., N.C., S.C., Tex.; Mexico; Central America; South America; Africa; Indian Ocean Islands (Madagascar).

Utricularia foliosa is found on the Atlantic and Gulf coastal plains. Reports of this species from North Carolina are based on P. Taylor (1989), but no specimens have been seen.

5. **Utricularia geminiscapa** Benjamin, Linnaea 20: 305. 1847

* Hidden-fruit bladderwort, utriculaire à scapes géminés **E**

Utricularia clandestina Nuttall ex A. Gray

Plants perennial, aquatic, submersed and free-floating, usually not tangled among other vegetation; turions globose-ovoid, 2--5 mm diam. **Stolons** monomorphic, green, little branched, terete, to 60 cm, 0.5--0.7 mm diam., leafy branches 1--3.5 cm diam.

Leaves alternate, very numerous, divided at base into 2 unequal primary segments, 10--20 mm, secondary segments repeatedly dichotomously divided (so leaves divided 6+ times), ultimate segments slightly flattened, shape filiform entire or sparsely and inconspicuously setulose, apex often bristle-tipped.

Bladders on leaves, scattered, sometimes dimorphic, (0.5--1)--2 mm. **Scapes** not subtended by inflated, floating branches, 5--25 cm; scales absent; bracts basifixed, green, linear, 2--3 mm, base not auriculate, apex acute; bracteoles 0. **Inflorescences**

racemes, 2--5(--8)-flowered (chasmogamous), with 1 or 2 apetalous cleistogamous flowers at very base of scape, opposite peduncle of chasmogamous flowers. **Pedicels** strongly ascending,

3--10(--20) mm (chasmogamous flowers), 0.5--2.5 mm (cleistogamous flowers). **Chasmogamous flowers:** calyx 1.5--2.5 mm; corolla yellow, not red-streaked or -veined, 7--10 x 3.5--5.5 mm; lower lip distinctly 3-lobed, lateral lobes not saccate,

lateral margins spreading; upper lip ascending, broadly ovate, unlobed, shorter and narrower than lower lip, apex mostly truncate (or rounded); palate prominently raised, densely pubescent; spur yellow, cylindrical, slightly curved, 2--3 mm, nearly as long as lower lip; apex obtuse. **Cleistogamous flowers** 1.5--2.5 mm diam.; corolla absent. **Capsules** globose, 1.5--3 mm (chasmogamous), 1.8--2 mm (cleistogamous), wall thin, membranous, dehiscence circumscissile.

Flowering Jul--Sep. Quiet waters of lakes, ponds, bogs, swamps, sluggish streams; 0--400 m; N.B., Nfld. and Labr. (Nfld.), N.S., Ont., P.E.I., Que.; Conn., Del., Ind., Maine, Md., Mass., Mich., N.H., N.J., N.Y., N.C., Ohio, Pa., R.I., Vt., Va., W.Va., Wis.

6. Utricularia gibba Linnaeus, Sp. Pl. 1: 18. 1753 *

Humped bladderwort, utriculaire à bosse

Utricularia biflora Lamarck; *U. exoleta* R. Brown; *U. fibrosa* Walter; *U. fornicata* Leconte; *U. gibba* subsp. *exoleta* (R. Brown) P. Taylor; *U. longirostris* Leconte; *U. obtusa* Swartz; *U. pumila* Walter; *Vesiculina gibba* (Linnaeus) Rafinesque

Plants annual or perennial, aquatic, flowering only when plant becomes stranded with drop in water level, or if plant becomes entangled among floating vegetation at water surface; turions

globose-ovoid, 1 mm diam., consisting of few loosely integrated leaves forming coiled leaf tips. **Stolons** not radiating from inflorescence base, monomorphic, green, much branched, often coiled at growing tips, often creeping over substrate or vegetative portion buried in wet mud/sand when stranded after drop in water level, delicate, terete, usually to 30 cm, 0.2--1 mm wide. **Leaves** alternate, very delicate, filiform, slightly flattened, 5--15 mm, divided dichotomously usually 2--4(--8) times, ultimate segments short, hairlike. **Bladders** on leaves, scattered, dimorphic, 0.3--0.8 mm and 1--1.6 mm. **Scapes** solitary or in pairs, not subtended by inflated, floating branches, slender, 0.3--1.3 cm; scales present or absent, basifixed, 0.8--1.3 mm; bracts basifixed, green, clasping pedicel, 0.5--1.5 mm, base not auriculate, margins entire, apex truncate; bracteoles 0. **Inflorescences** racemes, (1 or)2 or 3(--6)-flowered. **Pedicels** erect or spreading, (3--5)--10 mm. **Flowers:** calyx green, 2--4 mm, margins entire; corolla yellow, without conspicuous veins but with red-streaks on palate, both lips oriented upward, giving saddle-like appearance, (4--5)--17 x 4--13 mm; lower lip usually 3-lobed, sometimes unlobed, lateral lobes not saccate, lateral margins spreading; upper lip broadly ovate to nearly round, 3-lobed, slightly larger than lower lip, apex rounded to truncate; palate prominent, 2-humped,

densely pubescent; spur yellow, broadly conic, straight, (2--)3--4(--5) mm, shorter than to equal length as lower lip, apex blunt, or (southeastern coastal plain United States) cylindrical, straight or slightly curved, tapering to apex, 6--7(--8) mm, slightly shorter to slightly longer than lower lip, apex +/- acute or slightly blunt (sometimes strongly curved and well-developed in bud). **Capsules** globose, 2--4(--5) mm, wall membranous, dehiscence bivalvate. **2n** = 28.

Flowering Feb--Oct (mid Jul--Sep in north). Shallow water of lakes, ponds, pools, swamps, marshes, bogs, ditches, sluggish streams; 0--400 m; B.C., N.B., N.S., Ont., Que.; Ala., Ark., Calif., Conn., Del., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., N.H., N.J., N.Y., N.C., Ohio, Okla., Oreg., Pa., R.I., S.C., Tenn., Tex., Vt., Va., Wash., W.Va., Wis.; Mexico; West Indies; Central America; South America; s Europe; Asia; Africa; Indian Ocean Islands (Madagascar); Pacific Islands (Hawaii, New Caledonia, New Zealand, Palau); Australia.

P. Taylor (1989) regarded *Utricularia gibba*, the most widely distributed species of the genus, and best treated as a single extremely variable species, with a pantropical/eastern North American distribution. Within the eastern United States and Canada, there appear to be two fairly distinct infraspecific

entities, which can be distinguished only when in flower.

“True” *U. gibba*, described from Virginia and widely distributed in the cool-temperate northeastern North America and extending into the southeast primarily in the Piedmont, tends to have smaller flowers, 5--9(--12) x 4--6 mm, with spurs (2--3--4(--5)) mm, shorter than to same length as the lip, more broadly conic, straight, and blunt at the apex. Plants of this complex along the Atlantic and Gulf coastal plain, traditionally recognized as *U. biflora*, have somewhat to considerably larger flowers, 11--17 x 6--13 mm, with spurs 6--7(--8) mm, slightly shorter to slightly longer than the lower lip (strongly curved in bud) and more slender, cylindric, straight or slightly curved, tapering to a somewhat acute or slightly blunt. Additionally, a number of specimens from the Coastal Plain have been misidentified as belonging to *U. gibba* (*U. biflora*), but represent the terrestrial phase of *U. striata* (see comments under that taxon).

The taxonomy of *Utricularia gibba*, in the broad sense, is further confused by also having a pantropical phase.

Interestingly, some populations occurring in western North America (California, western Oregon, western Washington, and southwestern British Columbia), having smaller flowers (4--8 mm) with narrowly conic spurs that clearly exceed the lower corolla lobe, are very similar to plants collected in Costa Rica and

Bolivia, thus appearing to have strongest affinity with the pantropical phase of *U. gibba*, and may be introduced in western North America. Taylor (1961, 1964), studying *Utricularia* in Africa, treated the neotropical plants as subsp. *gibba* (including *U. biflora* and *U. obtusa*), and incorporated *U. exoleta* R. Brown of the Old World Tropics (Asia and Australia) as *U. gibba* subsp. *exoleta* (R. Brown) P. Taylor, with both subspecies occurring widely in Africa. Later (1989) he abandoned recognition of any infraspecific taxa for this highly variable, widespread species. It might be reasonable to recognize three infraspecific taxa, preferably at the subspecific rank: a north-temperate "true" *U. gibba* occurring throughout northeastern North America, a southeastern United States coastal plain "*U. biflora*" entity (which may include plants of the Caribbean described from Jamaica as *U. obtusa*, a name formerly used widely for *U. gibba* plants of the Neotropics), and a highly variable pantropical taxon ("*U. exoleta*" type); however, Taylor's concept of the species is retained here.

7. *Utricularia inflata* Walter, Fl. Carol., 64. 1788 *

Floating bladderwort, large swollen bladderwort **E**

Plectoma inflata (Walter) Rafinesque; *Utricularia ceratophylla*
Michaux

Plants annual or perennial, aquatic. **Stolons** robust, to 100 cm, 2--3 mm diam. (vegetative portion submersed, often breaking off from fertile portion below whorl of floats when collected).

Leaves alternate, along submersed vegetative stolons, immediately divided into unequal primary segments, much-branched, bushy, ultimate segments threadlike. **Bladders** on leaves, abundant, scattered, dimorphic, 0.7--1 mm and 1.5--2(--3) mm. **Scapes** 10--18 cm (above floats), subtended by whorl of 5--8(--10) large, inflated branches (floats) 3--8 cm; individual float branches cylindrical, margins gradually tapering to scape; main stem stout, 2--3 mm diam. (at 5 cm proximal to floats); scales absent; bracts basifixed, narrowly ovate, 3.5--5 mm, apex acute; bracteoles 0. **Inflorescences** racemes, (3--9)--14(--18)-flowered. **Pedicels** ascending, strongly recurved in fruit, 10--35 mm. **Flowers:** calyx 3--5(--6) mm; corolla bright yellow with red streaks or dots on palate, 12--18 x 15--20 mm; lower lip deeply 3-lobed, lateral lobes not saccate; upper lip orbicular, unlobed, equal to slightly smaller than lower lip, apex rounded; palate saccate, 2-humped, wrinkled, glabrous, spur yellow to greenish yellow, with reddish to brownish lines, conic, curved upward, 6--9 mm, 1/2 as long as lower lip, apex distinctly

notched. **Capsules** globose, (3--4--5(--6) mm, wall thick, fleshy, dehiscence circumscissile. **2n** = 18, 36.

Flowering Jan--Jun (Aug--early Sep Pacific Northwest).
Ponds, lakes, swamps, sloughs, ditches, canals; 0--200 m; Ala., Ark., Conn., Del., Fla., Ga., Ky., La., Maine, Md., Mass., Miss., N.J., N.Y., N.C., Okla., Pa., S.C., Tenn., Tex., Va., Wash.

Utricularia inflata is found chiefly on the Atlantic and Gulf coastal plains, but also extends inland. When sterile specimens are encountered, the vegetative submersed branches of *U. inflata* can be confused for *U. foliosa*, but the latter has a distinctive flat stem that is readily discerned in the field.

An introduction in the vicinity of Olympia, Washington, was encountered as early as 1980 (*Ceska & Ceska 4913*, WTU) and is now known from four counties in western Washington.

8. *Utricularia intermedia* Hayne, J. Bot. (Schrader) 1800(1):

18, plate 5. 1800 * Flatleaf bladderwort, utriculaire intermédiaire

Lentibularia intermedia (Hayne) Nieuwland & Lunell; *Utricularia intermedia* var. *robbinsii* Alph. Wood; *U. robbinsii* (Alph. Wood) Alph. Wood

Plants perennial, aquatic or anchored, spreading flat over surface of substrate, sometimes stranded on substrate as water recedes; turions oblong, 7--11(--15) mm, conspicuously setulose with white bristles on margins of scalelike leaves (appearing whitish on herbarium specimens). **Stolons** dimorphic: some whitish, usually unbranched, sometimes appearing anchored in loose substrate, others green, leafy, flat, to 30 cm, 0.4--0.6 mm diam. **Leaves** alternate, flat, 10--20 mm, slightly longer than wide, segments flat, +/- same width throughout, ultimate segments flat, margins toothed, teeth (5--9--12(--20)), setulose, apex +/- obtuse, sometimes setulose (bristles sometimes in fascicles of 2--4), midvein visible; leaf segments of submersed aquatic growth form strongly filiform. **Bladders** only on whitish stolons, (1.5--2.5--5.5) mm. **Scapes** not subtended by inflated, floating branches, (5--9--20) cm; scales present, basifixed, 2.2--3 mm, base conspicuously auriculate; bracts basifixed, 2.5--3.2 mm, base conspicuously auriculate, margins translucent, apex acute; bracteoles 0. **Inflorescences** racemes, (2 or) 3--5-flowered. **Pedicels** erect, 4--17 mm. **Flowers:** calyx 2.5--4 mm; corolla bright yellow with red veins on inner surface of upper lip and sometimes with red veins on summit of palate extending into tube, 8--18 x 8--15(--18) mm; lower lip unlobed; upper lip ascending, broadly ovate, unlobed,

1/2 length of lower lip, apex rounded; palate rounded, glabrous; spur sometimes marked with red veins, +/- appressed to lower lip, slender-cylindric, straight, narrowed, constricted at base (junction with tube), 4--7 mm, shorter than lower lip, apex acute. **Capsules** globose, 2.5--3 mm, wall firm textured, dehiscence circumscissile.

Flowering late May--Sep. Shallow pools and ponds, bog mats, peaty soils, wet sands, interdunal swales; 0--3400 m; Greenland; St. Pierre and Miquelon; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., Que., Sask., Yukon; Alaska, Ark., Calif., Colo., Conn., Idaho, Ill., Ind., Iowa, Maine, Md., Mass., Minn., Mont., Nev., N.H., N.J., N.Y., N.Dak., Ohio, Oreg., Pa., R.I., Utah, Vt., Wash., Wis., Wyo.; Eurasia.

Plants of *Utricularia intermedia* often occur in the submersed aquatic phase in early summer in deeper water, frequently in great abundance, having strongly filiform leaves; the distal portion of plant often reddish (superficially appearing as submerged *Myriophyllum humile*). Such plants are never seen flowering. The species can be recognized in the aquatic phase by the presence of dimorphic stolons---stolons with green filiform leaves bearing no bladders, and separate

whitish bladder-bearing stolons. Flowers only occur on plants that have been stranded on substrate surfaces.

9. Utricularia juncea Vahl, Enum. Pl. 1: 202. 1804 *

Southern bladderwort

Stomoisia juncea (Vahl) Barnhart; *S. virgatula* (Barnhart)

Barnhart; *Utricularia virgatula* Barnhart

Plants perennial, semiaquatic/semiterrestrial. **Stolons** numerous (but rarely collected), not radiating from inflorescence base, developing a delicate branch system within substrate, filiform, to several cm, ca. 0.2 mm diam. **Leaves** arising singly (often not seen), narrowly linear, terete, gradually tapering to a long point when submerged, when stranded becoming more straplike, flattened toward tip, or often withering away. **Bladders** on stolons, rhizoids, and leaves, subterranean, 0.3--0.6 mm.

Scapes greenish purple to purple, slender-wiry, 11--32 cm, 0.4--1 mm diam. near base; scales several to numerous, basifixed, 1.5--2.6 mm; bracts basifixed, purple, narrow, (0.7--1.5)--2.3 mm, margins entire; bracteoles 2, linear, 1.5--2 mm, as long as bracts. **Inflorescences** racemes, appearing spicate, several--many-flowered, elongate, flowers usually widely spaced along scape. **Pedicels** erect, 0.5--1.5 mm (flowers nearly sessile or pedicel as long as or longer than bracts). **Flowers:** calyx

green, (2.5--3--4(--4.8) mm, margins entire; corolla yellow, without conspicuous veins, 9--15 x 9--12 mm; lower lip unlobed; upper lip with sides curved backward, broadly obovate to orbiculate from a narrow base, unlobed, smaller than lower lip, apex rounded to sometimes truncated palate comprising most of lower lip, broadly humped or hood-shaped, pubescent; spur yellow, strongly divergent from lower lip, not clearly distinct from tube, conic, slender, straight or slightly curved, 4--6(--7) mm, longer than lower lip, apex long-tapering to acute.

Capsules globose to pyriform, 2.5--3(--3.5) mm, wall thick, hard, dehiscence by 1 longitudinal adaxial slit. **2n** = 18.

Flowering May--Oct. Shallow water, bogs, sandy-peaty margins of ponds, wet pine savannas and flatwoods, sandy alluvium, seepages, peaty ditches; 0--200 m; Ala., Del., Fla., Ga., La., Md., Miss., N.J., N.Y., N.C., Okla., S.C., Tex., Va.; e Mexico; West Indies; Central America; n South America; Africa (Ivory Coast).

Utricularia juncea is found primarily on the Atlantic and Gulf coastal plains, but also extends somewhat inland.

10. *Utricularia minor* Linnaeus, Sp. Pl. 1: 18. 1753 *

Lesser bladderwort, utriculaire mineure

Lentibularia minor (Linnaeus) Rafinesque

Plants perennial, aquatic; turions globose, 3--4 mm, not setulose, a few fine bristles at leaf tips, appearing naked, green. **Stolons** +/- dimorphic: usually some whitish, subterranean, others green, leafy, flat, slender, usually creeping flat on surface of substrate, or suspended in water, to 30 cm. **Leaves** alternate, flat, 2--8 mm, dichotomously-palmately divided (2--)3--4(--6) times, segments flat, +/- same width throughout, ultimate segments flat, margins entire or, if sparsely denticulate, then only microscopically setulose, sometimes segments very slender to filiform, apex acute, with or without minute bristle-tip, midvein visible. **Bladders** primarily on whitish stolons in substrate, few on ultimate lateral leaf segments, 0.7--1.5(--2.5) mm. **Scapes** not subtended by inflated, floating branches, 5--24 cm; scales present, purplish, basifixed, 1--1.5 mm, base conspicuously auriculate; bracts basifixed, purplish, (1--)1.5--2 mm, base conspicuously auriculate, apex acute or obtuse, bracteoles 0. **Inflorescences** racemes, 2--6(--10)-flowered. **Pedicels** ascending, recurved in fruit, 4--8 mm. **Flowers:** calyx 1.3--2 mm; corolla pale yellow with purplish tinge or stripes near base of lower lip, 3.5--8 x 2--3 mm; lower lip rounded or apex with slight notch, lateral margins strongly recurved; upper lip broader than long, apex with slight notch, less than 1/2 length of lower lip, apex

shallowly notched; palate obscure, elongate, with slightly raised lateral margins, glandular distally; spur not well defined, often red-veined, saccate or broadly conic, broad at base (junction with tube), 1.5--3.2 mm, 1/5--1/4 as long as lower lip, apex blunt. **Capsules** globose, 2--3 mm, wall firm, dehiscence circumscissile. **2n** = 36--40, 40, 44 [Europe].

Flowering May--Sep. Acidic shallow waters of lake margins, bog pools, marshes, wet meadows; 30--3400 m; Greenland; St. Pierre and Miquelon; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., P.E.I., Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Conn., Del., Idaho, Ill., Ind., Iowa, Maine, Mass., Minn., Mo., Mont., Nebr., Nev., N.H., N.J., N.C., N.Dak., Ohio, Oreg., Pa., R.I., S.Dak., Utah, Vt., Wash., Wyo.; Eurasia.

Populations of *Utricularia minor* are often encountered only in the vegetative state. It is a circumboreal species.

11. *Utricularia ochroleuca* R. W. Hartman, Bot. Not. 1857(2):

30. 1857 * Northern bladderwort, utriculaire jaunâtre **F**

Utricularia occidentalis A. Gray; *U. stygia* G. Thor

Plants perennial, aquatic, suspended or anchored with leafy branches creeping flat over surface of substrate; turions globose-ovoid, weakly setulose, (1.5--)2--3(--3.5) mm, appearing

naked, green. **Stolons** dimorphic: some whitish, usually within substrate, others green, leafy, flat, to 20 cm. **Leaves** alternate, flat, 2--7 mm, as wide as long, segments flat but very slender, +/- same width throughout, ultimate segments flat, margins usually sparsely toothed with (1--3--6--9) teeth, rarely entire, weakly setulose (bristles as long or longer than teeth, but very slender and obscure, even with magnification), apex acute, bristle-tipped, midvein visible. **Bladders** primarily on whitish stolons, 0 or 1(--2) on lateral segments of green leaves, 1--2.2(--3.8) mm. **Scapes** not subtended by inflated, floating branches, 5--17 mm; scales present, green, basifixed, 1.3--1.9 mm, base conspicuously auriculate; bracts basifixed, green, clasping pedicel, 1.5--3 mm, base conspicuously auriculate, apex acute; bracteoles 0. **Inflorescences** racemes, (2 or)3--5(--10)-flowered. **Pedicels** erect, 5--8 mm. **Flowers:** calyx 1.6--2.6 mm; corolla light to pale yellow, often with red veins on palate, 8--11 x 7--13 mm; lower lip unlobed, lateral margins nearly flat to slightly curved upward or slightly deflexed; upper lip ascending, broadly ovate, unlobed, 1/2 length of lower lip, apex rounded; palate prominent, rounded, glabrous; spur often streaked with red veins, at 45°-90°-angle to lower lip, short-conic to short conic-pyramidal, usually straight, broad at base (junction with tube), 2.2--3.5(--5.5)

mm, 1/2 as long as lower lip, apex +/- acute. **Capsules** unknown (ovary broadly ellipsoid). **2n** = 40, 44, 46, 48 [Europe].

Flowering Jun--Sep. Bogs, boggy meadows, marshes, often shallow water; 0--2400 m; Greenland; Alta., B.C., Man., Nfld. and Labr. (Labr.), Nunavut, N.W.T., N.S., Ont., Que., Yukon; Alaska, Calif., Colo., Mich., Mont., Ohio, Oreg., Wash., Wyo.; Eurasia; circumboreal.

Flowers of *Utricularia ochroleuca* vary in regard to streaking (presence of reddish streaks/veins, conspicuous to sometimes faint) or absence of streaks on the palate and spur. The spur is especially distinctive with its short-conic/pyramidal shape and 45°-90°-angle orientation (in contrast to *U. intermedia* with its spur appressed to and only slightly shorter than the lower lip, and constricted near base of spur). Vegetatively, the bladders are often borne on the flat green leaf segments as well as on separate white, non-photosynthesizing, stolons (whereas in *U. intermedia*, the bladder traps are borne only on the colorless shoots or very rarely with a few occurring on leaves). Turions of *U. ochroleuca* appear naked, whereas the densely packed turion leaves of *U. intermedia* are conspicuously setulose, appearing whitish on herbarium specimens.

Utricularia ochroleuca, regarded as a species of hybrid origin with purported *U. intermedia* and *U. minor* parentage, appears to be a vegetative apomict, persisting and dispersing via turions (P. Taylor 1989). When in flower, the taxon is more readily recognizable, but it is not uncommon for populations to occur in the sterile/vegetative state, especially if in deeper water of streams and lakes, complicating identification. G. Thor (1988) employed morphology of the 4-fid trichomes lining the inner surface of bladder traps as taxonomic characters. B. J. Plachno and L. Adamec (2007) found the angle between the two shorter arms to be statistically most diagnostic. I have found this character reliable to distinguish *U. ochroleuca* (with mean angle 128.9° ; range $111\text{--}146^\circ$) from *U. intermedia* (with mean angle 28.6° ; range $16\text{--}42$ or arms closed/H-shaped) and from *U. minor* (shorter arms usually reflexed), but not from depauperate, sterile specimens of *U. vulgaris* subsp. *macrorhiza* (with short-arms mean angle 133.9° ; range $114\text{--}154^\circ$). A few populations from North America that appear to fit Thor's concept of *U. stygia* have 4-fids (somewhat X-shaped) that are intermediate between *U. intermedia* and *U. ochroleuca* (the most problematic populations occurring in northern California), but considering the variability observed, resolution will surely require applying molecular techniques. Meanwhile, it appears that

although *Utricularia stygia* may be worthy of recognition at some taxonomic rank, perhaps at the varietal or possibly the subspecific level, at the species level it is, at best, a "cryptic species." Therefore, until some more definitive study can be conducted, it is more practical to treat this group taxonomically in the broader sense, with *U. ochroleuca* having nomenclatural priority and *U. occidentalis* and *U. stygia* as synonyms. If recognized at the specific level, *U. occidentalis* appears to have nomenclatorial priority over *U. stygia*.

12. *Utricularia olivacea* C. Wright in A. H. R. Grisebach, Cat. Pl. Cub., 161. 1866 * Piedmont bladderwort, pygmy bladderwort

Biovularia olivacea (C. Wright) Kamienski

Plants annual, aquatic, minute, delicate, becoming entangled with other aquatic plants or stranded as water recedes, and then more likely to flower. **Stolons** monomorphic, green, coiled at growing tips, branched, and often forming suspended mats, filiform, a few cm, 0.05--0.1 mm diam. **Leaves** (or leaflike branchlets) absent. **Bladders** numerous, on stolons, 0.4--0.7 mm. **Scapes** not subtended by inflated, floating branches, extremely short (0.1--0.2 mm, appearing absent); scales absent; bracts basifixed, clasping pedicel, 0.5--0.7 mm, apex truncate or

erose; bracteoles 0. **Inflorescences** racemes, 1--5-flowered, flowers often solitary. **Pedicels** erect, 0.5--5 mm. **Flowers:** calyx 0.5--0.7 mm; corolla creamy-white-translucent, (1--2--2.3--3.5) mm diam.; lower lip emarginate or weakly 2--3 lobed, lateral lobes not saccate; upper lip broader than long, unlobed, 1/3--1/2 length of lower lip, apex truncate to rounded or slightly emarginate; palate slightly raised, indistinct, glabrous; spur creamy-white, very short, base of lower lip more saccate than forming a distinct spur. **Capsules** fusiform, 1--1.1 mm, wall thin, indehiscent.

Flowering Aug--Oct. Ponds, lakes, sloughs, shallow ditches; 0--200 m; Ala., Fla., Ga., N.J., N.C., S.C., Va.; West Indies (Cuba); Central America (Nicaragua); South America.

Utricularia olivacea, which is found on the Atlantic and Gulf coastal plains, is undoubtedly overlooked, partly because of the diminutive nature of the vegetative plant body and tiny flowers, and partly because flowering tends to occur only when the plants are stranded on the wet substrate when water recedes or when the plants become greatly entangled with other aquatic species, allowing the plants to grow at the surface (much as is the case with *U. gibba*).

13. Utricularia purpurea Walter, Fl. Carol., 64. 1788 *

Eastern purple bladderwort, utriculaire pourpre

Vesiculina purpurea (Walter) Rafinesque

Plants perennial, aquatic; turions poorly developed, thickened, 1--2 mm diam., with strongly incurled leaf tips. **Stolons**

delicate, elongate, to 60+ cm, 0.5--1.5 mm diam. **Leaves**

whorled, stalked, with repeatedly divided whorls of thinner

segments, ultimate segments filiform. **Bladders** only at tips of

leaf segments, 1.5--2.5(--2.8) mm. **Scapes** borne along stolons

near surface at irregular intervals (plants often remaining

vegetative), stout, 2.5--10(--21) cm; scales absent; bracts

peltate, attached near base with shorter lower lobes extending beyond point of attachment, clasping pedicel, 2--3.5 mm;

bracteoles 0. **Inflorescences** racemes, 2 or 3(--5)-flowered

(usually 1 flower open at a time). **Pedicels** erect, 5--20 mm.

Flowers: calyx 2--2.5(--3) mm; corolla usually light purple to deep purple or pink with white-bordered yellow blotch on palate,

rarely all white, 5--15(--18) x 6--14 mm; lower lip 3-lobed,

lateral lobes conspicuously saccate, central lobe nearly square and strongly deflexed along margins, apex truncate and slightly

notched; upper lip convex, nearly orbiculate, unlobed, ca. 2/3

to slightly smaller than lower lip; apex rounded or shallowly

notched; palate not prominently raised (confluent with saccate

lateral lobes), papillate; spur same color as rest of corolla, conic to short-cylindric, (2--4--6 mm, distinctly shorter than lower lip, enclosed by enrolled lateral margins of central lobe, apex blunt. **Capsules** rare, globose, 3--4 mm, walls thin, membranous, dehiscence by 1 longitudinal adaxial slit.

Flowering Feb--Oct. Acidic waters of ponds, lakes, swamps, quiet waters of slow streams, sloughs, ditches; 0--400 m; N.B., Nfld. and Labr. (Nfld.), N.S., Ont., Que.; Ala., Conn., Del., Fla., Ga., Ill., Ind., La., Maine, Md., Mass., Mich., Minn., Miss., N.H., N.J., N.Y., N.C., Pa., R.I., S.C., Tex., Vt., Va., Wis.; Mexico; West Indies; Central America (Belize, Nicaragua).

14. Utricularia radiata Small, Fl. S.E. U.S., 1090. 1903 *

Little floating or small swollen bladderwort **E**

Utricularia inflata Walter var. *minor* Chapman, Fl. South. U.S., 282. 1860

Plants annual or perennial, aquatic; vegetative portion submersed, delicate, (often breaking off from fertile portion below whorl of floats when collected); turions globose, to 1 mm diam. **Stolons** filiform, to 50 cm, 0.3--1 mm diam. **Leaves** alternate, along submersed vegetative stolons immediately divided into 2 equal primary segments, these less densely branched than in *U. inflata*, not appearing bushy, ultimate

segments filiform. **Bladders** on leaves, abundant, scattered, monomorphic, 1.5--2 mm. **Scapes** 3.5--11 cm (above floats), subtended by whorl of (4 or)5--7(--10) inflated branches (floats), 1--4 cm; individual float branches cylindrical, margins parallel entire length until just before scape; main stem very slender, 0.3--0.7(--1) mm diam. (at 5 cm proximal to floats); scales absent; bracts basifixed, clasping pedicel, oblong, 2--3 mm, apex +/- 3-lobed; bracteoles 0. **Inflorescences** racemes, (1--3 or 4(or 5)-flowered. **Pedicels** ascending, rarely recurved in fruit, 2--18 mm. **Flowers:** calyx 2.5--3.5 mm; corolla dull yellow with red streaks or spots on palate, 8--20 x 5--10 mm; lower lip deeply 3-lobed, lateral lobes not saccate; upper lip nearly orbiculate, unlobed, +/- same size as lower lip, apex rounded; palate saccate, distinctly 2-humped, glabrous or with short papillae; spur yellow with red lines (veins), conic to cylindrical, 4.6--6 mm, shorter than lower lip, apex rounded, rarely with slight notch. **Capsules** globose, 3--5 mm, wall thick, fleshy, dehiscence circumscissile. **2n** = 28.

Flowering Feb--Oct. Ponds, lakes, swamps, quiet waters of slow-moving rivers, drainage ditches; 0--200 m; N.B., N.S.; Ala., Ark., Conn., Del., Fla., Ga., Ind., La., Maine, Md., Mass., Mich., Miss., N.H., N.J., N.Y., N.C., Okla., Pa., R.I., S.C., Tenn., Tex., Vt., Va.

Utricularia radiata is chiefly found on the coastal plains and the Mississippi embayment, with few known inland localities.

15. *Utricularia resupinata* B. D. Greene ex Bigelow, Fl.

Boston ed. 3, 10. 1840 * Lavender bladderwort, utriculaire
résupinée **E** **F**

Lecticula resupinata (B. D. Greene ex Bigelow) Barnhart

Plants perennial, semiaquatic/semiterrestrial; vegetative parts anchored in substrate, often mat-forming. **Stolons** branched, filiform, to 20+ cm, ca. 0.15 mm diam. **Leaves** arising singly, linear-subulate to filiform, 40--110 cm, distinctly septate (sometimes septa only 1--2, toward apex). **Bladders** numerous, on leaves and stolons, dimorphic, bladders on threadlike stolons 0.2--0.5 mm, larger traps (0.6--0.8--1(--1.5) mm. **Scapes** 4--20 cm (including pedicel); scales absent; bracts basifixed, 2, opposite, connate basally, 1.2--2.5 mm; bracteoles 0.

Inflorescences solitary flowers. **Pedicels** erect, 9--25 mm.

Flowers tipped backward, appearing upside-down; calyx 2--3 mm; corolla usually light purple to rose-pink with yellow spot on palate, rarely completely white, 5--13(--17) x 5--11 mm; lower lip usually ascending, obscurely 3-lobed; upper lip ascending, very narrowly oblong-obovate, unlobed, ca. 1/3 width of lower lip; lower lip broadly cuneate with apex crenulate; palate

prominent, wrinkled, glabrous, spur darker than rest of corolla, purple-lavender, cylindrical or narrowly conic, with a pronounced saccate swelling at base, conspicuously curving upward or away from scape, 3.5--6 mm, 1/2 as long as lower lip, apex blunt to truncate or slightly notched. **Capsules** globose, 2.5--3(--4) mm, wall firm, dehiscence by 1 longitudinal adaxial slit. **2n** = 36.

Flowering Mar--Dec (Aug--Sep in north). Sand and mud in shallow water of pools, ponds, lakes, river shores, ponds in open pine savannas and flatwoods; 0--400 m; N.B., N.S., Ont., Que.; Ala., Conn., Del., Fla., Ga., Ind., Maine, Md., Mass., Mich., Minn., N.H., N.J., N.Y., N.C., Pa., R.I., S.C., Tenn., Vt., Wis.

16. Utricularia simulans Pilger, Notizbl. Königl. Bot. Gart. Berlin 6: 189. 1914 (as *simulaus*) * Fringed bladderwort

Plants perennial, semiaquatic/semiterrestrial. **Stolons** branching within substrate, delicate, a few cm, ca. 0.2 mm diam. **Leaves** in rosettes, emergent, lamina linear, gradually tapering to base, apex obtuse to acute. **Bladders** numerous on stolons within substrate, some on leaves, 0.2--0.3 mm. **Scapes** 5--15 cm; scales present, basifixed, 1.1--1.5(--2.2) mm, base slightly auriculate, margins strongly fimbriate; bracts basifixed, green, 1--1.5 mm, base slightly auriculate, margins fimbriate;

bracteoles 2, borne at summit of pedicel, 2--4 mm, larger than bracts, similar to and about same size as calyx (can be confused with calyx), base not auriculate. **Inflorescences** racemes, appearing spicate, 2--10-flowered, often congested, flowers +/- clustered distally. **Pedicels** to 1 mm. **Flowers:** calyx red, especially fimbriae, 2.2--4.5 mm, margins fimbriate; corolla yellow, 3--7 x 5--8 mm; lower lip unlobed; upper lip broadly ovate, unlobed, ca. 1/2 length of lower lip, apex rounded; palate prominent, papillate; spur same color as rest of corolla, conic, distinctly flattened horizontally, 2--4.2 mm, as long as lower lip, apex acute to obtuse. **Capsules** globose to pyriform, 1--2.3 mm, wall thin, firm, dehiscence by 1 longitudinal adaxial slit.

Flowering Aug--Nov. Acidic, sandy substrates, wet pine flatwoods and savannas; 0--20 m; Fla.; Mexico (Chiapas), West Indies (Cuba); Central America (Belize); South America; Africa.

Utricularia simulans is widely distributed in tropical Africa and South America, reaching northward in the Neotropics as scattered populations into the Caribbean and southern two-thirds of peninsular Florida. The name *Utricularia fimbriata* of various authors, but not of Kunth, has been applied to *U. simulans*.

17. Utricularia striata Leconte ex Torrey, Cat. Pl. New York,
89. 1819 * Striped bladderwort **E**

Trilobulina striata (Leconte) Rafinesque

Plants perennial, appearing aquatic with vegetative portions submersed in shallow water, becoming stranded when water recedes, then appearing semiaquatic/semiterrestrial and anchored in wet substrate. **Stolons** dimorphic: numerous whitish, delicate, subterranean, often with short rhizoids (especially along upper portion), bearing numerous subterranean leaves, others green, submersed, leafy, cylindric branches (foxtail-like), to 10 cm, 1--1.5(--2) cm diam.; terrestrial phase with stolons radiating from base of inflorescence, whitish, bearing short rhizoids (frequently severed when collected). **Leaves** alternate, dimorphic, subterranean leaves short, asymmetrically divided to 4 times, photosynthetic leaves highly divided, segments fine, terete, narrower beyond each dichotomy, ultimate segments filiform, midvein not visible. **Bladders** numerous and scattered on subterranean leaves, absent or few on green, non-subterranean leaves, 0.7--2 mm. **Scapes** not subtended by inflated, floating branches, erect, slender-wiry, (9--12--32) cm, 1 mm diam.; scales present, basifixed, 1.2--2.5 mm; base not auriculate; bracts basifixed, green, broadly obovate, 1.1--2.5 mm, base not auriculate, margins entire, apex obtuse; bracteoles

0. **Inflorescences** racemes, 1--4-flowered. **Pedicels** ascending, 10--30 mm. **Flowers:** calyx green, 2.7--3.5 mm, margins entire; corolla pale yellow to greenish yellow with conspicuous veins (especially in dried specimens) and red streaks at base of lower lip and usually on palate, continuing into spur, (10--15--22 x 10--17 mm; lower lip unlobed or weakly 3-lobed, lateral lobes not saccate; upper lip nearly reniform, nearly equal to lower lip, apex shallowly 3-lobed; palate prominent, 2-lobed, densely pubescent; spur yellow with red streaks extending into spur from lower lip, narrowly cylindrical or conic, nearly straight, (5--6--9 mm, 3/4 as long as to slightly longer than lower lip, apex usually shallowly notched, sometimes obscurely 3-lobed (appearing entire when pressed laterally). **Capsules** globose, 3--4.7 mm, wall thin, fleshy, dehiscence bivalvate. **2n** = 28.

Flowering Mar--Oct. Ponds, pools, swamps, wet peats, sandy shores; 0--200 m; Ala., Ark., Conn., Del., Fla., Ga., La., Md., Mass., Miss., N.J., N.Y., N.C., Pa., R.I., S.C., Tex., Va.

According to P. Taylor (1989), the name *Utricularia fibrosa* has been applied widely to *U. striata*, but his careful interpretation of Walter's descriptions of Carolinian *Utricularia* species led him to conclude that *U. fibrosa* is conspecific with *U. biflora*, a name placed in synonymy under *U. gibba*.

Utricularia striata typically flowers during March through July. Plants becoming stranded following a drop in the water table can be readily confused with the terrestrial form of the Atlantic and Gulf coastal plain phase of *Utricularia gibba* ("*U. biflora*"), but if vegetative portions of the plant are present, the two are easily distinguished. The terrestrial phase of *U. striata* can be recognized by the presence of several whitish subterranean stolons at the base of the inflorescence (radiating downward on specimens) bearing tiny rhizoids near the summit of the stolons. Additionally, the flowers are larger, typically having red streaks (veins) on the palate and at the base of the lower lip, extending into the spur, with the spur notched.

This species is found primarily on the Atlantic and Gulf coastal plains. It is documented from a single site in Butte County, California, where it was collected in 1974 (Ahart 497, CAS, OSC). It appears to have been a chance introduction there, perhaps a weed associated with rice cultivation in that area, but does not appear to have become naturalized there.

18. *Utricularia subulata* Linnaeus, Sp. Pl. 1: 18. 1753 *

Zigzag bladderwort

Enetophyton cleistogamum (A. Gray) Niewland; *Setiscapella cleistogama* (A. Gray) Barnhart; *S. subulata* (Linnaeus) Barnhart;

Utricularia cleistogama (A. Gray) Britton; *U. setacea* Michaux;
U. subulata var. *cleistogama* A. Gray; *Vesiculina setacea*
(Michaux) Rafinesque

Plants annual, semiaquatic, very small; vegetative parts anchored in wet substrate. **Stolons** numerous, not radiating from inflorescence base, branched, filiform, several cm, 0.1--0.2 mm diam. **Leaves** arising singly (usually not visible when flowering), lamina narrowly linear, 30--40 x 0.2--0.6 mm, gradually tapering to base. **Bladders** on stolons and leaves (usually remaining within substrate when plants collected, seldom on herbarium specimens), 0.2--0.5 mm. **Scapes** filiform-wiry, 4--18 cm; scales present, peltate, 0.6--1.1 mm; bracts peltate, green, appressed, clasping pedicel, 0.6--1(--1.5) mm, margins entire, bracteoles 0. **Inflorescences** racemes, (1 or)2--4(--8)-flowered. Pedicels ascending, 2--10 mm. **Flowers:** calyx green, 1--2(--2.5) mm, margins entire; corolla yellow, without conspicuous veins, 4--9 x 3--9 mm; lower lip 3-lobed; upper lip ovate unlobed, smaller than lower lip, apex rounded to acuminate; palate prominent, 2-lobed, pubescent, spur often reddish, appressed to lower lip, conic, (2.5--)3--5(--7) mm, slightly shorter than to slightly longer than lower lip, apex acute to rounded to sometimes slightly denticulate. **Capsules**

globose, 1.5--3.5 mm, wall thin, firm, dehiscence by ovate adaxial pore. $2n = 30$.

Flowering Mar--Oct. Open areas of wet pine savannas and flatwoods, bogs, clearings of swampy woods, peaty sands or marly wet soils, wet ditches; 0--200 m; N.S.; Ala., Ark., Calif., Del., D.C., Fla., Ga., Ind., La., Md., Mass., Mich., Miss., Mo., Nebr., N.J., N.Y., N.C., Okla., Pa., R.I., S.C., Tenn., Tex., Va.; Mexico; West Indies; Central America; South America; Asia; Africa; Indian Ocean Island (Madagascar); Australia.

Utricularia pusilla Vahl is similar to *U. subulata* but differs by having scapes bearing sterile bracts and a spur two times as long as the lower lip. *Utricularia pusilla* occurs in southern Mexico (north to Vera Cruz) and the West Indies, and therefore might be expected to occur in southern Florida.

19. *Utricularia vulgaris* Linnaeus, Sp. Pl. 1: 18. 1753 F

Subspecies 2 (1 in the flora): North America, nw Mexico, Europe, n Asia.

Subspecies *vulgaris* is found in Europe.

19a. *Utricularia vulgaris* Linnaeus subsp. *macrorhiza* (Leconte ex Torrey) R. T. Clausen, Cornell Univ. Agric. Exp. Sta. Mem.

291: 9. 1949 * Common bladderwort, greater bladderwort,
utriculaire vulgaire **F**

Utricularia macrorhiza Leconte ex Torrey, Cat. Pl. New York 11.
1819; *Lentibularia vulgaris* (Linnaeus) Moench var. *americana* (A.
Gray) Nieuwland & Lunell; *U. vulgaris* var. *americana* A. Gray

Plants perennial, aquatic, submersed and free-floating, usually
not tangled among other vegetation; turions ovoid, 10--20 mm
diam., strongly setulose. **Stolons** monomorphic, green, branched,
leafy branches 3--12 cm diam., terete, to 100+ cm, 0.5--1.5 mm
diam. **Leaves** alternate, very numerous, often divided at base
into 2 unequal primary segments, 15--90 mm, secondary divisions
pinnate, further divisions dichotomous (so leaves divided 6+
times), ultimate segments numerous, filiform, slightly
flattened, margins entire or toothed, conspicuously setulose,
apex bristle-tipped. **Bladders** on leaves, dimorphic, those
arising from near bases of secondary leaf divisions 1--5 mm,
those somewhat scattered on subsequent divisions minute. **Scapes**
not subtended by inflated, floating branches, 10--40 cm; scales
present, similar to bracts; bracts basifixed, green, 3--7 mm,
base slightly cordate or weakly to distinctly auriculate;
bracteoles 0. **Inflorescences** racemes, (3--)6--15-flowered (all
flowers chasmogamous, cleistogamous flowers absent). **Pedicels**
ascending at anthesis, recurved in fruit, 8--15 mm. **Flowers:**

calyx 3--5 mm; corolla bright yellow with red or reddish brown veins at apex of palate, 11--18 x 8--12 mm; lower lip unlobed, lateral margins strongly deflexed or spreading; upper lip ascending, broadly ovate, unlobed, slightly shorter than lower lip, apex truncate or slightly notched; palate prominently swollen, densely pubescent; spur with red veins, broadly conic at base, tapering to cylindrical distal portion, curved upwards, 4--9 mm, as long as lower lip, apex acute. **Capsules** globose, 5--6 mm, wall firm, dehiscence circumscissile. **2n** = 40, 44.

Flowering late May--early Sep. Quiet waters of lakes, ponds, bogs, swamps, sluggish streams; 0--1700 m; St. Pierre and Miquelon; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., Que., Sask., Yukon; Ala., Alaska, Ariz., Ark., Calif., Colo., Conn., Del., D.C., Idaho, Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Mo., Mont., Nebr., Nev., N.H., N.J., N.Mex., N.Y., N.C., N.Dak., Ohio, Okla., Oreg., Pa., R.I., S.Dak., Tenn., Tex., Utah, Vt., Va., Wash., W.Va., Wis., Wyo.; Mexico (Baja California); n Asia.

Treated here as subsp. *macrorhiza*, this taxon has been widely treated as distinct at the species level from the European *Utricularia vulgaris*, but the differences are largely associated with the spur. In the European taxon, the spur is 2.5--6(--8) mm, shorter than the lower lip, with a broad conic

base and tapering to a narrowly cylindrical or narrowly conic, blunt to somewhat acute apex, and typically straight (sometimes somewhat concave or convex), and internal glands are present only on the dorsal surface of the spur. In contrast, subsp. *macrorhiza* has a spur as long as the lower lip, 4--7(--9) mm, basally more narrowly conic, with the cylindrical distal portion clearly curved upward, and with an acute apex; internal glands are present on both dorsal and ventral surfaces. In both taxa the internal glands are usually not visible on herbarium specimens, and spurs must be dissected in fresh material for glands to be seen. When fruiting, both subspecies have recurved pedicels, while the sepals are somewhat to strongly divergent. The European subsp. *vulgaris* is vegetatively less robust, but P. Taylor (1989) acknowledged that the two cannot be distinguished vegetatively. While subsp. *macrorhiza* has been known to extend into northeast Asia, Taylor noted that it was not clear to what extent either subsp. *macrorhiza* (as *U. macrorhiza*) or subsp. *vulgaris* occurred in western Siberia. During field work in the region of Siberia west of Novosibirsk and in the Altai Mountains, I found that the Siberian material was indistinguishable from our American taxon, and recent reexamination of that Siberian material confirmed that those specimens belong to subsp. *macrorhiza*. Hence, subsp. *macrorhiza*

appears to be geographically more widely distributed than subsp. *vulgaris*. It is noteworthy that no infraspecific taxa were recognized by Taylor for any species in his worldwide monograph, hence his inclination to recognize *U. vulgaris* and *U. macrorhiza* as distinct species, a reasonable, practical approach when addressing nearly 230 species of *Utricularia*.

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